

Biological control of cat's claw creeper, *Macfadyena unguis-cati* (L.) A.H.Gentry (Bignoniaceae), in South Africa

A.M. King*, H.E. Williams & L.G. Madire

Agricultural Research Council-Plant Protection Research Institute, Private Bag X134, Queenswood, 0121 South Africa

The exotic vine *Macfadyena unguis-cati* (L.) A.H.Gentry (Bignoniaceae), cat's claw creeper, has become a significant threat to the biodiversity of a variety of sensitive ecosystems in South Africa. Owing to the nature of the infestations, as well as the difficulties and prohibitive costs associated with both mechanical and chemical controls, biological control is considered to be the most practical and sustainable means of successfully managing the weed in South Africa. The biological control programme against *M. unguis-cati* was initiated in 1996 and resulted in the release of *Charidotis auroguttata* Boheman (Coleoptera: Chrysomelidae: Cassidinae). Despite repeated releases, initial rates of establishment were low. Where successfully established, populations of the beetle have been slow to build-up, leading to only limited impact on the weed. Prompted by this lack of success, as well as the high potential for further spread of the weed, additional natural enemies were sought. Two lace bugs, *Carvalhotingis visenda* Drake & Hambleton, and *Carvalhotingis hollandi* Drake (Hemiptera: Tingidae), a leaf-mining beetle *Hylaeogena (Hedwigiella) jureceki* Obenberger (Coleoptera: Buprestidae), a leaf-tying moth *Hypocosmia pyrochroma* Jones (Lepidoptera: Pyralidae) and a seed-feeding weevil *Apteromechus notatus* (Hustache) (Coleoptera: Curculionidae) were subsequently imported into quarantine in South Africa for host-specificity testing. With the exception of *A. notatus*, all have been approved for release and are exhibiting promising initial rates of establishment and damage at a number of field localities. Impact studies have shown that cat's claw creeper is susceptible to sustained herbivore pressure.

Key words: biological weed control, insect natural enemies, foliar feeding, agent efficacy, climatic effects, management.

INTRODUCTION

The exotic perennial vine, *Macfadyena unguis-cati* (L.) A.H.Gentry (Bignoniaceae) (Fig. 1), also known as cat's claw creeper, is a significant threat to biodiversity in a number of regions of South Africa. Originally a native of Central and tropical South America, including the West Indies, the vine has become naturalized on every continent except Antarctica (Starr & Starr 2008). This extensive range has been facilitated through the horticultural trade which distributed the plant as an ornamental (Sparks 1999; Downey & Turnbull 2007; Starr & Starr 2008). Showy yellow flowers coupled with its climbing habit make the fast-growing creeper ideal to screen-off walls or unsightly buildings. The plant has become invasive in a number of countries including South Africa, Australia, China, the Cook Islands, India, Mauritius, New Caledonia, New Zealand, Réunion, Saint Helena, Vanuatu and the U.S.A., including Hawaii (Starr & Starr 2008).

Within South Africa, *M. unguis-cati* is still

considered to be in the early stages of invasion and although it is spreading, the current range is limited relative to its potential distribution as predicted by its climatic requirements (Rafter *et al.* 2008). Nevertheless, the weed has formed a number of very dense infestations and has become problematic in the Gauteng, Limpopo, Mpumalanga and North West provinces, and in some areas of the KwaZulu-Natal Province (Fig. 2). Using the climate comparison program CLIMEX, Rafter *et al.* (2008) constructed a model which predicted cat's claw creeper to be best suited to the climate over much of South Africa's southern and eastern coastline between latitudes 26°S and 33°S, and probably excluded from natural systems in the central and western regions of the country by both cold and dry stress. The model also predicted that the subtropical and tropical coastal areas of northern KwaZulu-Natal, a region as yet free of *M. unguis-cati* infestation, would be highly suitable for invasion.

Macfadyena unguis-cati is a woody, frost-tolerant,

*To whom correspondence should be addressed.
E-mail: kinga@arc.agric.za



Fig. 1. *Macfadyena unguis-cati*. (Drawn by M. Steyn, first published in Henderson (1995), ARC-Plant Protection Research Institute, Pretoria.)

structural parasite normally found associated with forest and riparian habitats (Raghu *et al.* 2006). Its distinctive leaves consist of two leaflets and a terminal three-forked tendril from which the vine draws its name. A tiny hardened hook on each fork can attach to most surfaces and thus enable the plant to 'climb' up walls, tree trunks and over other vegetation (Sparks 1999). This climbing habit enables the plant to form dense infestations in the canopy of trees where branches, and eventually entire trees, can be killed through a combination of both shading and weight (Downey & Turnbull 2007). In the absence of climbing support, stems readily grow along the ground and are capable of

forming a dense groundcover which precludes the growth and seed germination of indigenous understorey vegetation (Williams 2002; Downey & Turnbull 2007). In areas of introduction *M. unguis-cati* has become a significant invader of cultivated orchards and plantations, riparian corridors, natural forest remnants and disturbed areas such as roadsides and abandoned urban spaces (Williams 2002).

The management of cat's claw creeper is extremely difficult and little success has been achieved with either chemical or mechanical control in South Africa (Williams *et al.* 2008). Control is hampered by the weed's extensive and vigorous growth,

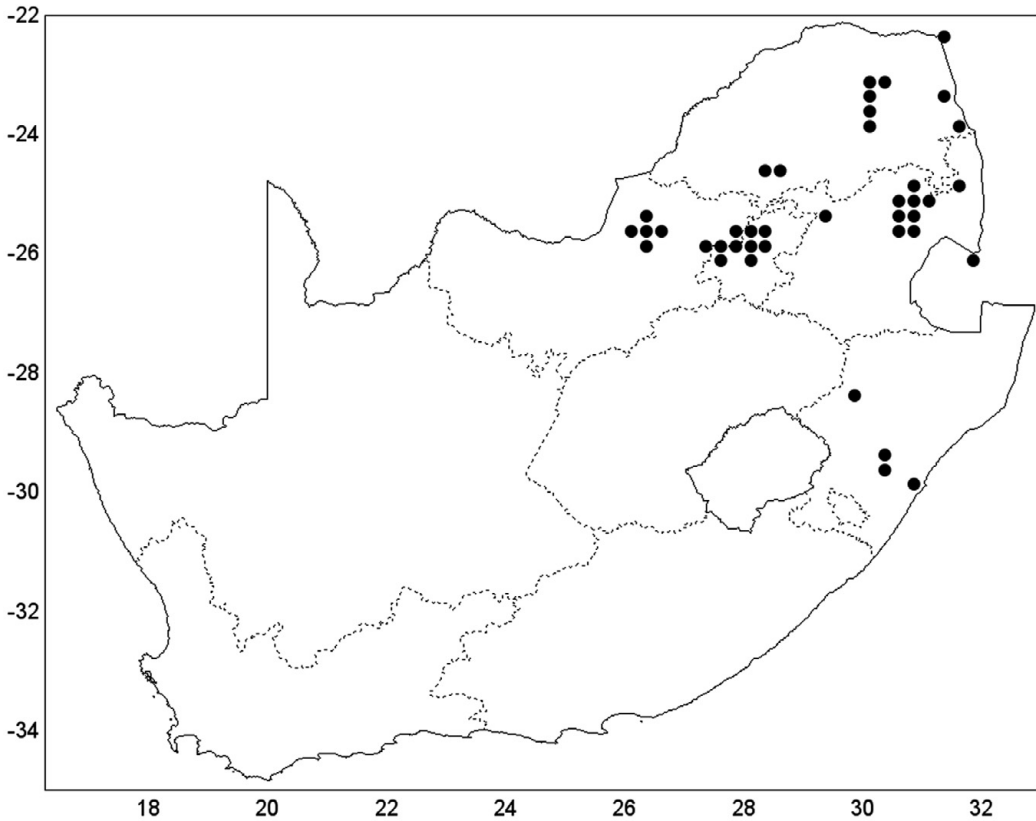


Fig. 2. Distribution of *Macfadyena unguis-cati* in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

profuse seed production and the presence of a network of underground root tubers. *Macfadyena unguis-cati* produces numerous flattened pod-like fruits, or capsules, each containing on average 90 winged seeds. Membranous wings on the seeds aid spread, which is predominantly facilitated by wind or water, making them well suited to dispersal down riparian corridors (Vivian-Smith & Panetta 2004; Downey & Turnbull 2007). Although seed production is high, Vivian-Smith & Panetta (2004) suggest that cat's claw creeper does not have a persistent seed bank. Seed longevity and seed bank densities were found to be low relative to similar invasive vines. However, the presence of tubers makes infestations extremely resilient as they readily re-sprout if aerial parts of the plant are damaged or removed, for example through mechanical removal or fire. Stems growing along the ground are also capable of producing roots and tubers at leaf nodes which form new plants if separated from the parent plant. This ability enables

the plant to withstand adverse conditions such as heavy frost and drought (King & Dhileepan 2009). Whilst spread is facilitated by seeds, the mechanism of persistence is predominantly through the tuber bank (Vivian-Smith & Panetta 2004; Osunkoya *et al.* 2009).

Any management strategy must therefore primarily target the tuber bank but also endeavour to remove mature vines in order to limit seed production and further spread (Vivian-Smith & Panetta 2004). Chemical control options are thus largely unsuccessful as they predominantly target above-ground growth and have little perceivable impact on the tuber bank. The use of chemical applications is further complicated by the risk of non-target effects. Broad-leaf herbicides can only be used selectively due to the propensity of cat's claw creeper to invade ecologically sensitive or economically important ecosystems (Sparks 1999; Dhileepan *et al.* 2005). Whilst some success has been achieved with mechanical and chemical

control (Downey & Turnbull 2007), because repeated follow-up is required, these techniques can only be used cost-effectively at very small scales. Weed management practitioners have thus prioritised biological control as the only practical and long-term solution to cat's claw creeper infestations. In this paper we review the current status of the biological control programme against *M. unguis-cati* in South Africa, in particular (i) the biology and host specificity of the six candidate natural enemies, (ii) the distribution and efficacy of these agents, and (iii) attempt to consolidate the work done since 1999 that has not yet been published.

THE BIOLOGICAL CONTROL AGENTS

Charidotis auroguttata Boheman (Coleoptera: Chrysomelidae: Cassidinae)

The biological control programme against *M. unguis-cati* in South Africa was initiated in 1996 by the Agricultural Research Council's Plant Protection Research Institute when nine potential agents were collected during surveys for natural enemies of other weeds of South American origin (Sparks 1999). Of the candidates collected, the golden-spotted tortoise beetle *C. auroguttata* was prioritised for introduction and screening owing to the narrow host ranges and specialized feeding habits normally attributed to the Cassidinae (Jolivet 1988). Under laboratory conditions *C. auroguttata* displayed a high rate of population increase which enabled the completion of several generations per year. It also exhibited good adult longevity and fecundity, and demonstrated high rates of both adult and larval feeding which resulted in considerable leaf skeletonization (Williams 2002). Permission for its release in South Africa was granted in 1999 and *C. auroguttata* became the first biological control agent released against cat's claw creeper anywhere in the world (Sparks 1999). Confronted with similar problems associated with *M. unguis-cati* infestations and buoyed by its anticipated efficacy and specificity under South African conditions, *C. auroguttata* was also imported into quarantine in Australia in 2001. Host-specificity testing, however, indicated that the beetle was prone to 'spillover' feeding on the Australian plant *Myoporum boninense* ssp. *australe* (Myoporaceae). The beetle was not considered for release even though it could not sustain viable populations on this species (Dhileepan *et al.* 2005).

Charidotis auroguttata was originally released at 13 sites in South Africa with very low initial rates of establishment despite repeated releases (Table 1). Where the beetle did establish, only minimal population build-up with correspondingly low levels of impact were evident and no signs of dispersal were recorded (Williams *et al.* 2008). The beetle's poor performance has been tentatively attributed to spider and ant predation, climatic mismatching (Williams *et al.* 2008), mistimed releases (H.E. Williams, pers. obs.), and parasitism of eggs, larvae or pupae (S. Nesar, pers. comm.).

Williams *et al.* (2008) suggested that because *C. auroguttata* is abundant throughout its native range, which encompasses several climatic regions throughout Argentina, Brazil and Venezuela, the beetle is unlikely to be hampered by climate in South Africa. This was further supported by the CLIMEX model constructed by Rafter *et al.* (2008). Through comparisons of several environmental stressors prevalent in the region from which the South African population of the beetle originates (Las Caracas, Venezuela) with those in South Africa, Rafter *et al.* (2008) showed that despite the latitudinal differences between the two regions, the beetle should be well suited to the climate over much of South Africa. Preliminary thermal tolerance work on *C. auroguttata* also suggested that the beetle is surprisingly cold-tolerant compared with other Cassidinae species from the same region (e.g. Byrne *et al.* 2002). The critical thermal minimum, the temperature below which adult beetles lost motor function, was calculated at 4.4 °C, and the lower lethal temperature, below which 50 % of the beetle population is expected to die, at -9.1 °C (A.M. King, unpubl.). Although *C. auroguttata* is cold-hardy and appears to be well suited to the climate throughout its area of introduction, additional studies are needed to investigate the effects, if any, of prolonged exposure to possibly less-than-optimal climatic conditions.

Additional biological control agents

As *M. unguis-cati* is present in gardens throughout South Africa (Sparks 1999), the potential for further spread of the weed is high. In the light of this and prompted by the lack of success of *C. auroguttata*, additional natural enemies were sought. Surveys between 2002 and 2009 yielded several insect species. Consequently, two lace bugs, *Carvalhotingis visenda* Drake & Hambleton, and *Carvalhotingis hollandi* Drake (Hemiptera:

Table 1. Details of releases of five biological control agents of *Macfadyena unguis-cati* released in South Africa and their current status.

Province/release site	Coordinates	Years of release	Number released/ Number of releases	Status
<i>Carvalhotingis hollandi</i>				
Gauteng				
Rietondale semi-field trial, Pretoria	25°43'S 28°14'E	2009–2010	440/2	Establishment confirmed
Limpopo				
Westfalia Estate, Tzaneen	23°43'S 30°06'E	2007	160/1	Not established
North West				
Riparian forest, Groot Marico	25°22'S 26°23'E	2010	800/1	Establishment unconfirmed
<i>Carvalhotingis visenda</i>				
Gauteng				
Broedestroom koppie, Johannesburg	25°51'S 27°52'E	2010–2011	2000/2	Establishment unconfirmed
Faerie Glen, Pretoria	25°47'S 28°19'E	2009–2011	2200/4	Not established
Florauna, Pretoria North	25°41'S 28°09'E	2010	1750/3	Establishment unconfirmed
Groenkloof Nature Reserve, Pretoria	25°46'S 28°11'E	2008; 2010–2011	5280/3	Establishment confirmed
Private garden, Johannesburg	26°16'S 28°00'E	2008	600/1	Not established
Private garden, Pretoria	25°46'S 28°16'E	2011	1000/1	Establishment unconfirmed
Rietondale semi-field trial, Pretoria	25°43'S 28°14'E	2009–2010	440/2	Establishment confirmed
Silverton Ridge, Pretoria	25°44'S 28°18'E	2010	1900/2	Establishment unconfirmed
KwaZulu-Natal				
Broadleaze Farm, Pietermaritzburg	29°37'S 30°25'E	2009–2010	2980/4	Establishment confirmed
National Botanical Gardens, Pietermaritzburg	29°36'S 30°20'E	2009	300/1	Establishment confirmed
Private garden, Pietermaritzburg	29°35'S 30°20'E	2009	220/1	Establishment confirmed
Limpopo				
Komatiland Forest, Tzaneen	23°46'S 30°07'E	2009	550/1	Establishment confirmed
Westfalia Estate, Tzaneen	23°43'S 30°06'E	2007	100/1	Not established
Roadside forest, Louis Trichardt	23°03'S 30°16'E	2010	3700/1	Establishment unconfirmed
Mpumalanga				
Private farm, White River	25°20'S 30°58'E	2010	1500/1	Establishment unconfirmed
North West				
Riparian forest, Groot Marico	25°24'S 26°22'E	2008–2010	2915/4	Establishment confirmed
Els Farm, Hartebeespoort	25°48'S 27°50'E	2009; 2011	1415/2	Establishment unconfirmed
<i>Charidotis auroguttata</i>				
Gauteng				
Broedestroom koppie, Johannesburg	25°51'S 27°52'E	2010	150/2	Establishment unconfirmed
Groenkloof Nature Reserve, Pretoria	25°46'S 28°11'E	2010	70/1	Establishment unconfirmed
Meintjieskop, Pretoria	25°43'S 28°14'E	1999	400/2	Establishment unconfirmed
Private garden, Johannesburg	26°05'S 28°00'E	2009	250/1	Not established
Private garden, Pretoria	25°43'S 28°14'E	2000–2001	730/3	Establishment unconfirmed
Rietondale tunnel, Pretoria	25°43'S 28°14'E	1999–2006	1200/16	Not established
Rietondale koppie, Pretoria	25°43'S 28°14'E	2000–2006	2000/8	Establishment confirmed
KwaZulu-Natal				
Broadleaze Farm, Pietermaritzburg	29°37'S 30°25'E	2010	200/1	Establishment unconfirmed
National Botanical Gardens, Pietermaritzburg	29°36'S 30°21'E	2001	1300/2	Establishment confirmed
SAPPI Buccleuch House, Pietermaritzburg	29°18'S 30°25'E	2000	230/1	Establishment unconfirmed
State Veterinary, Allerton, Pietermaritzburg	29°34'S 30°21'E	2000	175/1	Establishment unconfirmed
Limpopo				
Westfalia Estate, Tzaneen	23°43'S 30°06'E	1999–2000; 2007; 2009	720/8	Establishment confirmed
Mpumalanga				
Woodhouse Hall & Sons, Nelspruit	25°27'S 30°56'E	2000	300/1	Establishment unconfirmed
North West				
Avogro Farm, Rustenburg	25°47'S 27°19'E	2000	560/1	Establishment unconfirmed
Riparian forest, Groot Marico	25°24'S 26°22'E	2001–2002	720/2	Establishment confirmed
<i>Hylaeogena jureceki</i>				
Gauteng				
Broedestroom koppie, Johannesburg	25°51'S 27°52'E	2010	270/1	Establishment unconfirmed

Continued on p. 371

Table 1 (continued)

Province/release site	Coordinates	Years of release	Number released/ Number of releases	Status
Faerie Glen, Pretoria	25°47'S 28°19'E	2009–2010	830/2	Not established
Private garden, Johannesburg	26°16'S 28°00'E	2008–2009	510/2	Not established
Rietondale semi-field trial, Pretoria	25°43'S 28°14'E	2009–2010	440/2	Establishment confirmed
KwaZulu-Natal				
National Botanical Gardens, Pietermaritzburg	29°36'S 30°20'E	2008–2010	1605/4	Establishment confirmed
Private garden, Pietermaritzburg	29°35'S 30°20'E	2010	320/1	Establishment confirmed
Limpopo				
Westfalia Estate, Tzaneen	23°43'S 30°06'E	2007–2010	1925/5	Establishment confirmed
Barotta Fruit Farm, Louis Trichardt	23°03'S 30°16'E	2010	700/1	Establishment unconfirmed
<i>Hypocosmia pyrochroma</i>				
Gauteng				
Faerie Glen, Pretoria	25°47'S 28°19'E	2010–2011	1800/4	Establishment unconfirmed
Limpopo				
Westfalia Estate, Tzaneen	23°43'S 30°05'E	2010	600/1	Establishment unconfirmed

Tingidae), a leaf-mining beetle *Hylaeogena (Hedwigiella) jureceki* Obenberger (Coleoptera: Buprestidae), a leaf-tying moth *Hypocosmia pyrochroma* Jones (Lepidoptera: Pyralidae) and a seed-feeding weevil *Apteromechus notatus* (Hustache) (Coleoptera: Curculionidae) were imported into quarantine in South Africa for host-specificity testing (Williams *et al.* 2008). With the exception of *A. notatus*, the above species have been shown to be suitably host specific (Williams *et al.* 2008; H.E. Williams, unpubl.) and are discussed further below. Subsequent to the host-specificity work in South Africa, *C. visenda* and *H. pyrochroma* were imported into Australia for testing in 2004 and 2005, respectively. Both species were confirmed to be highly specific and were approved for release (Dhileepan *et al.* 2007a,b).

Carvalhotingis visenda and *Carvalhotingis hollandi*

Williams *et al.* (2008) described the biology, potential impact and host ranges of both these tingid species under quarantine conditions in South Africa. Colonies were established from material collected in 2002 near Curitiba in Brazil, and from Posadas in Argentina. *Carvalhotingis visenda* adults can be readily distinguished from *C. hollandi* by two distinctive, raised black knobs on the corium of each hemelytron. Females of *C. visenda* lay 6–37 eggs in batches along the main veins on the ventral surfaces of leaflets. Eggs are embedded in the leaf epidermis with only the opercula protruding, and are covered with a black substance which dries over the eggs. Eggs from

the same batch hatch simultaneously, on average after 13 days, and emerging nymphs feed gregariously on the underside of the leaves. Nymphs undergo five instars lasting 13–17 days. Adults and nymphs feed by sucking out the contents of the leaf parenchyma cells resulting in a distinctive white speckling on the leaves. Females lay between 50–460 eggs during their lifetime which can last up to 208 days.

Carvalhotingis hollandi, by contrast, lays 1–57 eggs and the batches are scattered in loose groups. The biology and life-history-stage durations of both tingids are very similar (Williams *et al.* 2008), and adults of both species display the same defence mechanism, dropping rapidly from leaves when disturbed. *Carvalhotingis hollandi* has a slightly longer pre-oviposition period, on average 17 days, five days longer than for *C. visenda*, and females were found to be more fecund, laying 266–544 eggs over their lifetime (Williams *et al.* 2008).

Host-specificity studies were conducted by exposing both species to several plant families during nymphal no-choice trials and adult multiple-choice trials (Williams *et al.* 2008). Test plant selection was done according to Wapshere's (1974) centrifugal phylogenetic testing method and included 23 representative species. Nine species in the family Bignoniaceae, seven species in closely-related families from the same order (Lamiales) as Bignoniaceae, and seven unrelated but economically important species with similar morphological or architectural characteristics, were included. The inclusion of several indigenous and non-indigenous ornamental climbers was deemed prudent in light

of the creepers' past popularity as an ornamental, and given that it is still present in gardens throughout South Africa. Under no-choice conditions, nymphs of both tingid species survived and completed their development on *M. unguis-cati* only. Adults from both species were similarly host specific and fed and oviposited exclusively on cat's claw creeper. The avoidance of egg-laying, coupled with a lack of immature development on any of the other test plants, was seen as a clear indication of suitable host specificity. Trial releases of both tingids are currently under way at selected field sites around the country.

Hylaeogena (Hedwigiella) jureceki

Colonies of *H. jureceki* were initially established from parent material collected in Argentina, Brazil and Paraguay and were imported into quarantine in South Africa in 2002. Although not found at particularly high population densities, the beetle was relatively widespread and common throughout this range (S. Nesar, pers. comm.). Adult beetles are 2 mm in length and black in colour with an irregular metallic sheen, and readily drop from the leaves if disturbed. Females lay numerous eggs singly on the ventral surfaces of leaflets, predominantly towards the leaf margin. Eggs are flat, transparent disks approximately 0.75 mm in diameter, which darken with age. Larvae emerge up to 12 days later and complete three instars whilst mining beneath the leaf epidermis. After approximately 25 days, larvae chew a distinctive circular disk into the leaf epidermis in which to pupate. Pupation lasts 7–11 days and after a pre-oviposition period of 12–22 days, emergent female beetles lay up to two eggs per day predominantly on the larger mature leaves at the base of the plant. Adult longevity is approximately nine months (H.E. Williams, unpubl.).

Host-specificity studies consisted of adult no-choice and multiple-choice tests (H.E. Williams, unpubl.). No-choice larval trials were not possible as larvae could not be successfully transferred from the leaf on which the egg had been laid, and host suitability was therefore determined by the ovipositing females. Plant selection tests were done in much the same manner as those for the tingids. Twenty-four representative plant species, 12 in the family Bignoniaceae, seven from closely related families in the Lamiales, and five unrelated but economically important species were used. During adult multi-choice trials, only cat's claw

creeper was found to be suitable for feeding and oviposition. Even under the deprived conditions of no-choice trials, no other test plant species was accepted for either feeding or oviposition. Trial releases of the beetle are currently under way at selected field sites around the country.

Hypocosmia pyrochroma

As in the case of *H. jureceki*, *H. pyrochroma* was first established in quarantine in South Africa from material collected in Argentina, Brazil and Paraguay in 2002. The moth was also found to be very widely distributed, abundant, and highly damaging to the vine throughout the areas surveyed (S. Nesar, pers. comm.). Adults are orange-brown in colour with distinct banding with white markings across the forewings. They are presumed to be nectar feeders. Eggs are pale green and laid singly on the leaves and stems of *M. unguis-cati*. Larvae hatch approximately 11 days after oviposition, develop through six instars and are exclusively foliar feeders. Larvae use silk to tie leaves together for concealment and wriggle vigorously if disturbed, which should afford them some resistance to predators, but seemingly little protection from parasitism. Numerous parasitoids (unidentified Braconidae, Bethyridae, Ichneumonidae (in the Hymenoptera), and Tachinidae (Diptera) have been recovered in field-collected material from South America. Feeding damage is extensive and larvae attack leaves of all ages. Once mature, larvae burrow 2–3 cm into the soil and pupation takes place in a tightly woven silk cocoon. Late-season pupae undergo winter diapause (Dhileepan *et al.* 2007a; H.E. Williams, unpubl.) making *H. pyrochroma* potentially able to withstand the adverse winter conditions prevalent in South Africa, especially over the interior high-lying regions of the country. Females are fecund and live on average for 10 days during which time they lay up to 120 eggs each.

Host-specificity testing consisted predominantly of larval no-choice trials and adult multi-choice trials (H.E. Williams, unpubl.). Test plant selection was performed in much the same manner as for the other insects and consisted of the same 24 plant species as for *H. jureceki*. During larval no-choice testing, only *M. unguis-cati* supported complete larval development. Some feeding and partial development was, however, observed on one other test plant species, *Markhamia obtusifolia* (Baker) Sprague (Bignoniaceae), but this did not extend beyond the second instar. Nevertheless, an

additional series of modified, larval choice trials and adult paired-choice trials were subsequently conducted. Larval choice trials were used to determine whether *M. obtusifolia*, if growing in close proximity to *M. unguis-cati* infestations supporting *H. pyrochroma*, could serve as an alternative host for the moth if the cat's claw creeper infestation was removed. Under these conditions, only 1.1 % of the larvae developed to pupation on *M. obtusifolia*. The partial development of the surviving larvae was likely aided by the initial presence of the true host plant as a source of high nutrition and was therefore not considered a true reflection of the moths' host range. During adult paired-choice trials only *M. unguis-cati* was suitable for oviposition and no eggs or larvae were found on *M. obtusifolia*. Similarly, none of the plants tested, other than *M. unguis-cati*, proved suitable for egg-laying during the adult multi-choice trials. In the light of this, the chances of *M. obtusifolia* supporting viable field populations of *H. pyrochroma*, given the extra biotic and abiotic pressures normally experienced under field conditions, are extremely small. The high degree of specificity exhibited by *H. pyrochroma* was further supported by work done in Australia. Host-specificity testing there involved 38 test plant species and demonstrated that cat's claw creeper only was a suitable host and the moth was duly approved for field release (Dhileepan *et al.* 2007a). *Hypocosmia pyrochroma* has recently been released in South Africa (Table 1) but establishment has not been confirmed.

IMPACT OF THE BIOLOGICAL CONTROL AGENTS

Foliar feeders

Williams *et al.* (2008) suggested that in order to manage *M. unguis-cati* successfully, biological control will need to target the plant's aggressive growth and vegetative spread, reduce persistence by targeting the tuber bank, and lessen further spread *via* sexual propagules by targeting flower and seed production. Simulated herbivory experiments have shown that defoliation has the potential to reduce the productivity of cat's claw creeper (Raghu *et al.* 2006). By simulating damage to young plants, Raghu *et al.* (2006) found that at least two severe defoliation treatments were needed to significantly reduce stem growth rate and tuber biomass accumulation. Simulated below-ground damage had a negligible impact on plant biomass

accumulation, and tuber damage elicited vigorous compensatory growth in the form of an increased tuber yield. In the light of these findings, Raghu *et al.* (2006) suggested that below-ground feeders should be avoided, and that foliar feeders were likely to be the most suitable for achieving control of cat's claw creeper. However, because the vines' performance was only reduced significantly in treatments where over 50 % of the leaves were removed, only extremely damaging insects, or natural enemies with high intrinsic rates of natural increase, will have the potential to severely affect the plant.

In quarantine, adults and nymphs of both *C. visenda* and *C. hollandi* feed gregariously, which leads to severe leaf chlorosis. Larvae of *H. jureceki* mine extensively, and in some cases, mines destroy entire leaflets. While these mines are most often restricted to the larger mature leaves, adult feeding is normally concentrated around younger growing points leading to leaf skeletonization. *Hypocosmia pyrochroma* larvae are voracious feeders and are able to consume large quantities of leaf tissue, leading to distinct transparent windows and in some cases leaf skeletonization. Feeding by these insects significantly reduces the amount of leaf area available to the plant for photosynthesis, and at high insect population densities, promotes premature leaf abscission and eventual stem growth-point die-back (King & Dhileepan 2009).

In a study to determine the potential efficacy of *C. hollandi* under laboratory conditions, Williams *et al.* (2008) found that nymphal feeding was capable of significantly reducing leaf chlorophyll content. However, no discernible decrease in stem growth, or any impact to either above- or below-ground biomass was detected during the same experiment. Similar results were obtained by Conrad & Dhileepan (2007) when testing the potential efficacy of *C. visenda* under quarantine conditions in Australia. A single generation of the tingid significantly reduced leaf chlorophyll content, but because the study ran for longer, a significant reduction in both plant height and leaf biomass was recorded. Again, however, no impact on the below-ground components, including the size and biomass of roots and tubers, was detected. Similarly, in a laboratory evaluation of the potential efficacy of *H. jureceki* at different population densities, where a significant reduction in leaf biomass was recorded after a single generation, no reduction in stem growth rate or below-ground biomass was

observed (H.E. Williams, unpubl.). Williams *et al.* (2008) speculated that with prolonged exposure to herbivory, the sustained loss of photosynthetic capacity and consequent reduction in available photosynthetic metabolites, could significantly affect plant biomass accumulation over the long term, which would be consistent with the predictions made by Raghu *et al.* (2006). Indeed, under semi-field conditions, sustained feeding from *H. jureceki* over two summer seasons, which culminated in the removal of an average of 67 % of the leaves per plant, resulted in a significant reduction in both above- (40 %) and below-ground (51 %) biomass (A.M. King, unpubl.).

Hypocosmia pyrochroma, by comparison, appears to be far more damaging than the tingids and *H. jureceki*. H.E. Williams (unpubl.) measured the impact of two generations of larval feeding at different densities under laboratory conditions in order to gauge the potential efficacy of the moth. After just 84 days, with varying population densities, significant reductions (27–78 %) in above-ground biomass were recorded relative to the controls. However, below-ground biomass was only significantly reduced (19–20 %) in treatments with high larval densities, emphasizing again the need for severe and sustained defoliation in order to reduce the plant's below-ground reserves.

These studies showed that *M. unguis-cati* is susceptible to high levels of foliar damage. Whether or not the field populations of these recently-released biological control agents will attain densities that are able to inflict these levels of defoliation, over the long term, remains to be seen. *Carvalhotingis visenda* has been actively released since 2008 but establishment has only been confirmed at 41 % of the release sites (Table 1). By contrast, Dhileepan *et al.* (2010b) reported *C. visenda* established at 80 % of release sites in Australia after a period of three years. Nevertheless, intense localized feeding indicated by severe leaf chlorosis has been recorded around many release points and random stem sampling has shown a significant increase in feeding over time at the majority of these sites. Particularly rapid population increases by the tingid at one of the release sites resulted in feeding damage on 95 % of all leaflets sampled, which caused stem-growth-point die-back and widespread leaf defoliation (51 %) (A.M. King, unpubl.). Simultaneous releases of *H. jureceki* at separate sites (Table 1) have, however, not provided the same level of population

increase as for *C. visenda*. As a result, where the beetle has established, foliar damage is minimal and no measurable impact on plant growth or biomass has been recorded. The beetle has nonetheless become widely dispersed at these sites, in one instance damaging leaves that were over 1.5 km from the initial release point (A.M. King, unpubl.).

Unfavourable climatic conditions within an area of introduction are often cited as limiting factors to the establishment and efficacy of insects introduced for biological control (*e.g.* Byrne *et al.* 2002; McClay & Hughes 2007). Dhileepan *et al.* (2010a) described the thermal physiology of *C. visenda*. Adults were found to tolerate a much wider range of temperatures (0–45 °C) relative to the nymphs (15–30 °C). Oviposition, egg hatching and nymphal development were all adversely affected by both high (>30 °C) and low (<20 °C) temperatures. Thus, unsuitable temperatures are anticipated to negatively influence the establishment of the tingid. Additionally, although only indirectly addressed during high temperature treatments, relative humidity was also cited as a possible limiting factor for the survival of the tingid under field conditions. Nevertheless, because cat's claw creeper normally occupies relatively sheltered habitats within forests and along riparian zones, Dhileepan *et al.* (2010a) suggested that microclimate effects could minimize the detrimental effects of these restricted tolerances to temperature and humidity. Dry and hot conditions which led to a decline in plant quality have hampered the field establishment of both *C. visenda* and *H. jureceki* at a number of relatively exposed sites in South Africa. Sheltered conditions, by contrast, coupled with artificial watering provided during semi-field evaluations, facilitated the successful establishment of *C. visenda*, *C. hollandi* and *H. jureceki*. Macroclimatic conditions during these evaluations were not dissimilar to those at field sites where establishment failed, but due to a favourable microclimate, the insects were able to persist. Where field establishment has been achieved, declines from high late-season densities have been recorded during the colder, drier winter months, but in protected microclimates, for example, relatively-closed riparian systems where soil moisture is retained, insect populations were able to recover once macroclimatic conditions improved (A.M. King, unpubl.). Fine-scale conditions prevalent at a site, which may be largely independent of broader macroclimatic trends, are therefore antici-

pated to play an integral role in determining insect establishment and persistence, and consequently, the level of control achieved against a given *M. unguis-cati* infestation.

Flower- and seed-feeding insects as potential agents

Although reductions in sexual reproductive potential are often associated with declines in plant reserves (Crawley 1989), defoliation of *M. unguis-cati* has not yet been linked to a reduction in flowering or seed set. The distribution of cat's claw creeper to new localities is undoubtedly enabled by seeds. Osunkoya *et al.* (2009) suggested that the recruitment of new plants around already-established infestations is also facilitated by seeds and not solely from the tuber bank as was previously thought. Future biological control efforts should therefore focus on acquiring and releasing specialist flower- and/or seed-feeding insects in order to reduce the weeds' seed output.

The seed-feeding weevil *A. notatus* has been found in relatively large numbers throughout the areas surveyed in Argentina, Brazil and Paraguay (S. Naser, pers. comm.). Adult beetles were imported but were not successfully cultured in quarantine. Adults are long lived (up to 22 months), mottled-brown in colour, on average 4 mm in length, and feed both on mature seeds and around the growth points of young *M. unguis-cati* stems. Eggs are laid singly and are normally embedded in the tissue of immature or green pods. Hatching larvae tunnel into the developing pods and feed on several seeds before pupating. Winter diapause takes place within the harder, mature pods, predominantly as pupae, and newly eclosed adults emerge in early spring so as to coincide with the next season's flowering and early pod growth (A.M. King, unpubl.). This long developmental duration, compounded by the weevil's close association with developing pods, presents a significant challenge in respect of rearing and host-specificity testing under quarantine conditions. As only mature vines produce flowers, techniques need to be developed to stimulate sexual reproduction in potted cat's claw creeper plants in order for the weevil to be successfully cultured and tested. Barring this, surveys of related Bignoniaceae, coupled with possible open-field trials in South America, could provide further evidence on the weevil's host range.

Within its native range, *A. notatus* larvae, often

three to five per capsule, have been observed destroying up to 80 % of the seeds within a single developing pod (S. Naser, pers. comm.). Crawley (1989), however, cautioned that seed-feeding insects can only impact a plants' population dynamics if its recruitment is naturally seed limited. In the case of *M. unguis-cati*, Vivian-Smith & Panetta (2004) reported that seed longevity is low and that field infestations maintain relatively low *in situ* seed bank densities. By limiting seed production, thus reducing seed bank replenishment, *A. notatus* might make a valuable contribution to the control of the weed.

CONCLUSIONS

Surveys and collections of natural enemies of *M. unguis-cati* have, up to now, been largely opportunistic and have been focused in Paraguay, northeast Argentina, and the southern reaches of Brazil (S. Naser, pers. comm.). Subsequently, Prentis *et al.* (2009) showed that introduced haplotypes of *M. unguis-cati* in many regions around the world, including South Africa, came from very few areas in the plant's native range. More than 96 % of introduced specimens were found to match a single haplotype from Paraguay. Logically, locally-adapted natural enemies collected from this dominant haplotype are anticipated to be best suited for introduction for biological control, and would avoid any difficulties that could arise from mismatching of host and agent (Prentis *et al.* 2009). However, by using climate matching, Rafter *et al.* (2008) predicted that in terms of climatic suitability, natural enemies collected in Paraguay would have limited potential as biological control agents in South Africa. The models used by Rafter *et al.* (2008) were not inclusive of many of South Africa's climatic regions currently infested with *M. unguis-cati*. Nevertheless, the refinement of these models, coupled with the knowledge of a dominant haplotype, could serve to direct future surveys and enhance the chances of finding more suitable natural enemies or biotypes should problems arise in the introduced range as a result of climatic mismatching.

Despite this, a suite of effective natural enemies have been identified, tested, and the performance of these agents is currently being studied in the field. Initial establishment and impact of the insects recently approved for release has been promising,

and bearing in mind the positive results already achieved in Australia with *C. visenda* (Dhileepan *et al.* 2010b), prospects for biological control of cat's claw creeper in South Africa are good. A wealth of information now also exists on the ecology of the vine, as well as its susceptibility to various modes of herbivore pressure. This work does, however, emphasize that only intense and sustained herbivore pressure will be able to significantly reduce cat's claw creeper infestations. For this reason, the biological control of *M. unguis-cati* in South Africa will require continual support in terms of novel research, release efforts, and long-term monitoring.

REFERENCES

- BYRNE, M.J., CURRIN, S. & HILL, M.P. 2002. The influence of climate on the establishment and success of the biocontrol agent *Gratiana spadicea*, released on *Solanum sisymbriifolium* in South Africa. *Biological Control* **24**: 128–134.
- CONRAD, K.A. & DHILEEPAN, K. 2007. Pre-release evaluation of the efficacy of the leaf-sucking bug *Carvalhotingis visenda* (Hemiptera: Tingidae) as a biological control agent for cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae). *Biocontrol Science and Technology* **17**: 303–311.
- CRAWLEY, M.J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* **34**: 531–564.
- DHILEEPAN, K., BAYLISS, D. & TREVIÑO, M. 2010a. Thermal tolerance and potential distribution of *Carvalhotingis visenda* (Hemiptera: Tingidae), a biological control agent for cat's claw creeper, *Macfadyena unguis-cati* (Bignoniaceae). *Bulletin of Entomological Research* **100**: 159–166.
- DHILEEPAN, K., SNOW, E.L., RAFTER, M.A., TREVIÑO, M., McCARTHY, J. & WILMOT SENARATNE, K.A.D. 2007a. The leaf-tying moth *Hypocosmia pyrochroma* (Lep., Pyralidae), a host-specific biological control agent for cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae) in Australia. *Journal of Applied Entomology* **131**: 564–568.
- DHILEEPAN, K., TREVIÑO, M., DONNELLY, G.P. & RAGHU, S. 2005. Risk to non-target plants from *Charidotis auroguttata* (Chrysomelidae: Coleoptera), a potential biocontrol agent for cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae) in Australia. *Biological Control* **32**: 450–460.
- DHILEEPAN, K., TREVIÑO, M. & SNOW, E.L. 2007b. Specificity of *Carvalhotingis visenda* (Hemiptera: Tingidae) as a biological control agent for cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae) in Australia. *Biological Control* **41**: 283–290.
- DHILEEPAN, K., TREVIÑO, M., BAYLIS, D., SAUNDERS, M., SHORTUS, M., McCARTHY, J., SNOW, E.L. & WALTER, G.H. 2010b. Introduction and establishment of *Carvalhotingis visenda* (Hemiptera: Tingidae) as a biological control agent for cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae) in Australia. *Biological Control* **55**: 58–62.
- DOWNEY, P.O. & TURNBULL, I. 2007. Review. The biology of Australian weeds 48. *Macfadyena unguis-cati* (L.) A.H. Gentry. *Plant Protection Quarterly* **22**: 82–91.
- HENDERSON, L. 1995. *Plant Invaders of Southern Africa*. Plant Protection Research Institute Handbook No. 5. Agricultural Research Council, Pretoria, South Africa.
- JOLIVET, P. 1988. Food habits and food selection of Chrysomelidae. Bionomic and evolutionary perspectives. In: Jolivet, P., Petitpierre, E. & Hsiao, T.H. (Eds) *Biology of the Chrysomelidae*. 1–20. Kluwer Academic Publishers, London, U.K.
- KING, A. & DHILEEPAN, K. 2009. Clinging on: A review on the biological control of cat's claw creeper. *Biocontrol News and Information* **30**: 53N–56N.
- McCLAY, A.S. & HUGHES, R.B. 2007. Temperature and host-plant effects on development and population growth of *Mecinus janthinus* (Coleoptera: Curculionidae), a biological control agent for invasive *Linaria* spp. *Biological Control* **40**: 405–410.
- OSUNKOYA, O.O., PYLE, K., SCHARASCHKIN, T. & DHILEEPAN, K. 2009. What lies beneath? The pattern and abundance of the subterranean tuber bank of the invasive liana cat's claw creeper, *Macfadyena unguis-cati* (Bignoniaceae). *Australian Journal of Botany* **57**: 1–7.
- PRENTIS, P.J., SIGG, D.P., RAGHU, S., DHILEEPAN, K., PAVASOVIC, A. & LOWE, A.J. 2009. Understanding invasion history: genetic structure and diversity of two globally invasive plants and implications for their management. *Diversity and Distributions* **15**: 822–830.
- RAFTER, M.A., WILSON, A.J., WILMOT SENARATNE, K.A.D. & DHILEEPAN, K. 2008. Climatic-requirements models of cat's claw creeper *Macfadyena unguis-cati* (Bignoniaceae) to prioritise areas for exploration and release of biological control agents. *Biological Control* **44**: 169–179.
- RAGHU, S., DHILEEPAN, K. & TREVIÑO, M. 2006. Response of an invasive liana to simulated herbivory:

ACKNOWLEDGEMENTS

We thank the *Working for Water* Programme and the Agricultural Research Council for continued financial support; S. Nesar for his valuable ideas and direction, as well as for the collection of insects in South America; and K. Dhileepan for additional financial support *via* the Department of Employment, Economic Development and Innovation, Biosecurity Queensland, Alan Fletcher Research Station, Australia which made the most recent overseas surveys possible. We are also grateful to F. Heystek for comments on an earlier draft of the manuscript.

- implications for its biological control. *Acta Oecologica* **29**: 335–345.
- SPARKS, H.E. 1999. The initiation of a biological control programme against *Macfadyena unguis-cati* (L.) Gentry (Bignoniaceae) in South Africa. In: Olckers, T. & Hill, M.P. (Eds) *Biological Control of Weeds in South Africa (1990–1998)*. *African Entomology Memoir* **1**: 153–157.
- STARR, F. & STARR, K. 2008. Ecology of *Macfadyena unguis-cati*. In: *Global Invasive Species Database*. Online at: <http://www.issg.org/database/species/ecology.asp?si=1227&fr=1&sts=&lang=EN> (accessed August 2010).
- VIVIAN-SMITH, G. & PANETTA, F.D. 2004. Seed bank ecology of the invasive vine, cat's claw creeper (*Macfadyena unguis-cati* (L.) A. Gentry). In: Sindel, B.M. & Johnson, S.B. (Eds) *Proceedings of the Fourteenth Australian Weeds Conference*. 531–534. Wagga Wagga, NSW, Australia.
- WAPSHERE, A.J. 1974. A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology* **77**: 201–211.
- WILLIAMS, H.E. 2002. Life history and laboratory host range of *Charidotis auroguttata* (Boheman) (Coleoptera: Chrysomelidae), the first natural enemy released against *Macfadyena unguis-cati* (L.) Gentry (Bignoniaceae) in South Africa. *The Coleopterists Bulletin* **56**: 299–307.
- WILLIAMS, H.E., NESER, S. & MADIRE, L.G. 2008. Candidates for biocontrol of *Macfadyena unguis-cati* in South Africa: biology, host ranges and potential impact of *Carvalhotingis visenda* and *Carvalhotingis hollandi* under quarantine conditions. *BioControl* **53**: 945–956.